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PREDATORY BEHAVIOR OF THREE JAPANESE SPECIES OF *METLEUCAUGE* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT

The predatory behavior of *Metleucauge kompirensis* (Boes. et Str.), *M. yunohamensis* (Boes. et Str.) and *Metleucauge* sp. was studied, and the natural prey of the former two species were collected from their webs. These species did not immobilize their prey by wrapping, but immobilized them only by biting. The lack of immobilization wrapping in *Metleucauge* can be explained by two different hypotheses: 1) *Metleucauge* remains in the primitive stage of the evolution of predatory behavior, or 2) the habit of immobilization wrapping has been lost, because *Metleucauge* captures weakly flying insects (mainly midges and mayflies) which can be immobilized without wrapping.

INTRODUCTION

It has been suggested that there are five stages in the evolution of predatory behavior in araneid spiders, judging mainly from whether immobilization wrapping is used or not (Robinson et al. 1969; Robinson 1975).

Robinson and his colleagues agreed with Eberhard (1967) that lack of immobilization wrapping is primitive, and immobilization wrapping is advanced. They supposed that immobilization wrapping was derived from post-immobilization wrapping (that is, the wrapping after immobilization by biting) at the capture site.

Alternatively, Levi (1985) suggested that the lack of immobilization wrapping in *Micrathena* and *Gasteracantha* is not a primitive character, but rather a secondary loss of immobilization wrapping.

Eberhard (1982) stated that immobilization wrapping evolved independently along three lines, Theridiosomatidae-Anapidae, Araneidae, and Tetragnathidae-Metinae. As examples of the spiders with immobilization wrapping in the Tetragnathidae-Metinae line, he listed *Dolichognantha* spp., *Leucauge* spp., and *Chrysometa* spp. *Tetragnatha praedonia* also sometimes uses immobilization wrapping with large prey (Yoshida 1987). The predatory behavior in the Tetragnathidae-Metinae line has been studied only fragmentarily, and no species without attack wrapping has yet been found.

Levi (1980) included Tetragnathidae in the Araneidae, and divided Araneidae into the three subfamilies (Araneinae, Metinae and Tetragnathinae). He included several genera, such as *Meta, Metellina, Metleucauge,* and *Leucauge*, in Metinae. He stated that *Meta* and the related genera have many primitive morphological characters, and that the genera resemble some genera of Theridiidae, a family of

Araneoidea. Recently, Levi (1986) divided Araneidae again into two families, Araneidae and Tetragnathidae, with the latter including Metinae and Tetragnathidae described in the previous paper.

I report here on the predatory behavior of the three Japanese species of *Metleucauge* (*M. kompirensis, M. yunohamensis*, and *Metleucauge* sp.). These species do not use immobilization wrapping at all. I also discuss the evolution of the predatory behavior in the Tetragnathidae-Metinae line.

Metleucauge sp. has been thought to be *Meta segmentata* previously by Japanese arachnologists. But Shinkai and Takano (1984) stated that it belongs to *Metleucauge*, and that they regarded it as *Metleucauge segmentata.* Recently, Yaginuma (1986) said that its species name is not *segmentata*, though it belongs to *Metleucauge.* He said that it resembles *M. yunohamensis*, but is a new species of *Metleucauge.*

MATERIALS AND METHODS

The investigation of *M. kompirensis* and *M. yunohamensis* was done in 1986 and 1987 at two mountain streams in Kyoto city (100-200 m above sea level). *M. yunohamensis* matured in April to May, and *M. kompirensis* matured in June to July. The species usually made their horizontal orb-webs above the mountain streams. I observed the predatory behavior of adults of the two species, both with natural prey and with the fairly large prey given by me. The latter prey were collected using a sweep-net near the study area. Less than two prey were attached to a web by a pincette. I observed predatory behavior of many individuals of *M. kompirensis* for several hundred hours, and of *M. yunohamensis* for several tens of hours. The body length of both the spiders and the prey was estimated by eye.

The third species, *Metleucauge* sp., was investigated halfway up Mt. Chougatake, north of Nagano Prefecture (ca 1400 m above sea level). This species, like *kompirensis* and *yunohamensis*, also usually made its web above mountain streams. I could observe the predatory behavior for only ten to several hours.

RESULTS

Predatory behaviors.—The following behaviors were observed in the context of predatory sequences:

Jerking: This consists of a rapid pulling of the radii with the first pair of legs.

Web-Shaking: Only *M. yunohamensis* showed this behavior. This species sometimes shook the web slowly with legs I (and II?) as soon as the prey hit the web. This is different from jerking, because the web was pulled perpendicularly to its plane. The function of the low frequency vibration is unknown.

Approach to prey: Running or walking from the hub to the capture site along the radial thread(s), pulling a drag-line from the hub. Running occurred generally when the prey was vibrating rapidly, while walking occurred generally when the prey was motionless (not vibrating).

Touch: The spiders touch the prey with legs I (and palps?) before most attacks are initiated. *Metleucauge* species often touched the prey with legs I in unsuccessful prey capture sequences, whereas touching was not observed at all in successful prey capture sequences. Touching might have occurred also in the latter case, but may have occurred too rapidly to detect without high-speed film.

Seizing in jaws: Seizing and holding the prey in the chelicerae.

Biting: Biting the prey with the chelicerae. Lubin (1980) included both seizing and biting in biting. Certainly the jaws are used both in seizing and biting, but there are some differences between them. Robinson and Robinson (1973) pointed out that seizing is used mainly with very small prey, whereas biting is used mainly with larger prey, and that the time required for seizing was very short, whereas the time required for biting was several times longer than that for seizing. So, I intend to distinguish seizing from biting.

Wrapping: Wrapping was used only after prey immobilization in *Metleucauge* species. Wrapping occurred at three sites: at the capture site, during transportation to the hub, and at the hub itself. At the capture site, wrapping generally began after immobilization biting while the prey was still in the spider's jaws. I called this type of wrapping, also observed in *Tetragnatha praedonia*, as "wrapping with bite" (Yoshida 1987). After "wrapping with bite", *Metleucauge* released the prey from its jaws, and then cast additional skeins of silk onto the prey. Wrapping was often interrupted by cutting the prey from the web. Free-wrapping (wrapping the prey beneath the web) was rarely observed. *Metleucauge* was different from *Argiope argentata*, because it never rotated the prey around a radius while wrapping ("rotisserie" wrapping of Eberhard [1982]).

Pulling out: Pulling the prey from the web, using the jaws.

Cutting out: Cutting the web in order to remove the prey from the web.

Carrying in jaws: Carrying the prey in the jaws to a feeding site.

Carrying on silk: Carrying the prey to the feeding site, suspended on a silk line from the spinnerets. The silk line made by *M. yunohamensis* was short, so the prey sometimes became entangled in the web. In these circumstances, the web was destroyed, as the spider pulled the prey out by force. Other species did not show this behavior.

Leaving the prey: The return of the spider to the hub alone, leaving the prey at the capture site.

Predatory sequences employed.—Three predatory sequences were observed in *M. kompirensis* and *M. yunohamensis* as follows:

Seize-Pull out: Spiders generally located prey by jerking the web, then ran to the prey, seized it in the jaws and pulled it from the web. Spiders then carried the prey in the jaws to the hub. In most cases, spiders returned by dropping from the web, hanging with the dragline attached to the hub, and then climbed quickly to the hub along the dragline ("drop and climb up" behavior). It took only 2-5 seconds for the spiders to complete seize-pull out sequences.

Bite-Pull out: This sequence resembles seize-pull out, the above sequence, but it includes the behavior unit "biting". The time to seize the prey was very short (perhaps less than one second), but biting took several seconds to several minutes. Probably spiders would infuse the venomous fluid into the prey during biting. Spiders usually bit some parts of a large prey first for a fairly long time (more than several seconds), and then they changed the biting sites successively. As a result, the prey was crushed gradually into a ball. Then the spider pulled it from the viscid spirals with the jaws. The prey were carried either by drop and climb-up mentioned above, or carrying the prey along a radial thread.

Bite-Wrap: The prey were immobilized by biting. After immobilization biting, spiders first wrapped the prey with silk while it was still in the jaws. Then they

Table 1.—Attack sequences with different types of prey in three species of *Metleucauge*. Frequency of occurrence of the different sequences is shown after each sequence.

Prey type	*M. kompirensis*		*M. yunohamensis*		*Metleucauge* sp.	
Diptera	Seize-Pull Out	54	Seize-Pull Out	4	Seize-Pull Out	0
	Bite-Pull Out	2	Bite-Pull Out	1	Bite-Pull Out	1
	Bite-Wrap	0	Bite-Wrap	11	Bite-Wrap	3
Ephemeroptera	Seize-Pull Out	18	Seize-Pull Out	0	Seize-Pull Out	0
	Bite-Pull Out	0	Bite-Pull Out	0	Bite-Pull Out	0
	Bite-Wrap	0	Bite-Wrap	5	Bite-Wrap	2
Lepidoptera	Seize-Pull Out	0	Seize-Pull Out	0	Seize-Pull Out	0
	Bite-Pull Out	1	Bite-Pull Out	0	Bite-Pull Out	0
	Bite-Wrap	12	Bite-Wrap	4	Bite-Wrap	1
Hymenoptera	Seize-Pull Out	1				
	Bite-Pull Out	0				
	Bite-Wrap	0				
Plecoptera	Seize-Pull Out	0			Seize-Pull Out	0
	Bite-Pull Out	0			Bite-Pull Out	0
	Bite-Wrap	1			Bite-Wrap	1
Odonata	Seize-Pull Out	0				
	Bite-Pull Out	4				
	Bite-Wrap	12				
Orthoptera	Seize-Pull Out	0				
	Bite-Pull Out	1				
	Bite-Wrap	0				
Neuroptera					Seize-Pull Out	0
					Bite-Pull Out	1
					Bite-Wrap	0

wrapped further after releasing it from the jaws. When the prey was large, wrapping was often interrupted by cutting the silk entangling the prey. The silk covered only some parts of the prey, perhaps because the amount of silk was little. Finally, spiders cut out all the entangling silk lines, in order to remove the prey from the web. In most cases, the prey were carried to the hub suspended on a silk line. *Metleucauge* sp. used bite-pull out and bite-wrap, but did not use seize-pull out.

Frequency of sequences with different types of prey and efficiency of predation on various types of prey.—Table 1 shows the comparison of attack sequences with different types of prey in three species of *Metleucauge*. The wrap-bite sequence, frequently used by *Argiope*, was not used by the spiders at all. With Diptera and Ephemeroptera, *M. kompirensis* used mainly seize-pull out and did not use bite-wrap at all, while *Metleucauge* sp. used mainly bite-wrap with Diptera and Ephemeroptera, and did not use seize-pull out at all. *M. yunohamensis* used only bite-wrap with Ephemeroptera, and used mainly bite-wrap with Diptera. Lepidoptera and Odonata were attacked mainly by bite-wrap.

Table 2 shows the efficiency of predation (% of prey insects captured to the total insects attached to the webs) on various types of prey in each species. Diptera, Ephemeroptera, and Lepidoptera were captured efficiently by all species, though few data are available for *Metleucauge* sp. Damselflies were captured efficiently also by *M. kompirensis*. Hemiptera (stink bugs and leafhoppers) was not captured at all. And Orthoptera and Hymenoptera was captured only once,

Table 2.—Efficiency of predation on various types of prey. Numerals show the number of prey captured or not captured by each spider species. Numerals in parentheses show the percentages.

	M. kompirensis		*M. yunohamensis*		*Metleucauge* sp.	
Prey type	Captured	Not Captured	Captured	Not Captured	Captured	Not Captured
Diptera	56 (91.6)	2(8.4)	16(100	0(0)	4(66.7)	2(33.3)
Ephemeroptera	18(100)	0(0)	5(100)	0(0)	2(100)	0(0)
Lepidoptera	12 (80.0)	3(20.0)	4(80.0)	1(20.0)	1(100)	0(0)
Odonata	16 (72.7)	6(23.3)	—	—	—	—
Hymenoptera	1 (50.0)	1(50.0)	0(0)	5(100)	0(0)	2(100)
Hemiptera	0(0)	5(100)	0(0)	3(100)	—	—
Orthoptera	1(10.0)	9(90.0)	—	—	—	—
Coleoptera	—	—	0(0)	3(100)	—	—
Plecoptera	1(100)	0(0)	—	—	1(100)	0(0)
Neuroptera	—	—	—	—	1(50.0)	1(50.0)
Mecoptera	—	—	—	—	0(0)	1(100)
Dermaptera	—	—	—	—	0(0)	1(100)
Lepidoptera (larva)	—	—	—	—	0(0)	2(100)
Total	105(80.1)	26(19.9)	25(67.6)	12(32.4)	9(50.0)	9(50.0)

respectively. When failing in prey-capture, the spider often touched the prey with leg(s) I.

The spiders failed to capture Hemiptera, Orthoptera, Hymenoptera and Coleoptera 28 times (93% of these insects given), and there were several types of failures: 1) spiders did not respond to the prey (four times), 2) the spider only jerked its web (once), 3) prey escaped before the spiders arrived at the capture sites (three times), 4) the spider approached its prey, but then returned to the hub, leaving the prey at the capture site (once), 5) spiders tried to bite the prey, but returned to the hub without biting (it is unknown why they did not bite: five times). Of these, one spider touched the prey before attempting to bite, and two spiders dropped the prey from the webs after attempting to bite, 6) spiders returned to the hub after prey-touching (nine times), 7) spiders dropped their prey after prey-touching (four times), 8) the spider bit its prey, but dropped it after prey-touching (once).

Prey-touching was observed with 54% (15/28) of the insects not captured, very often with Hemiptera (7/8), but was not observed at all with Coleoptera (0/3). This behavior occurred mainly before returning to the hub alone and prey-dropping (13/15). This prey-touching behavior was not observed at all when the spider succeeded in capturing the prey.

Figs. 1-3 show the relation between the relative body length (prey/spider) and the predatory sequences employed in each species. Seize-pull out was used with very small prey (smaller than half a spider body length or so), while bite-wrap was used mainly with larger prey. Bite-pull out, whose frequency was low, was used with prey of intermediate size.

Figs. 1-3 also show the relative body length of prey insects not captured by spiders. It ranged widely. In some cases, such as Diptera, Lepidoptera, Hymenoptera, Orthoptera (the prey of *M. kompirensis*), Neuroptera (the prey of *Metleucauge* sp.), the insects that escaped were larger than ones captured, suggesting that larger prey cannot be captured easily. However, the prey insects that escaped from webs of *Metleucauge* sp. were smaller than ones captured. In

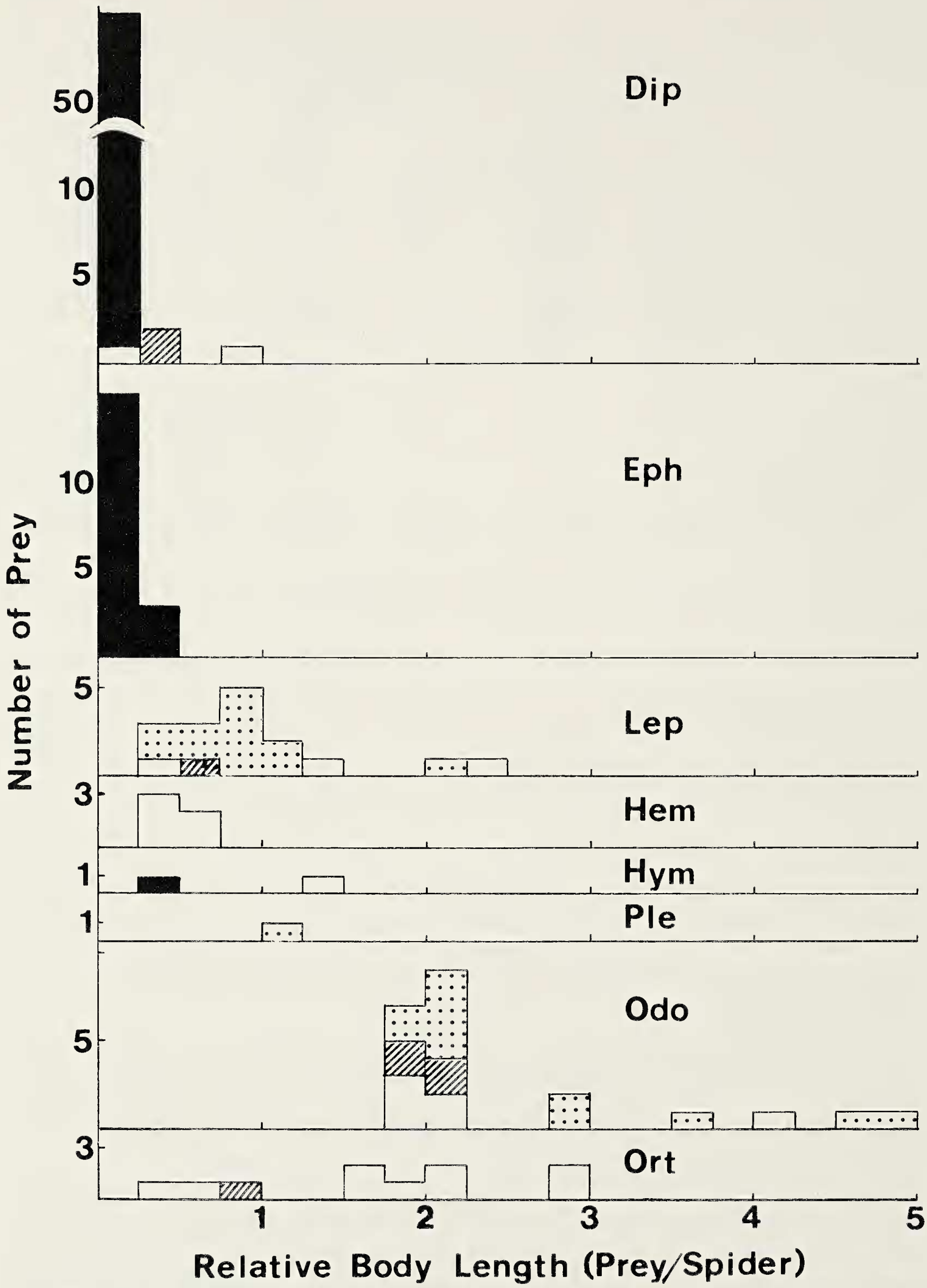

Figure 1.—The relation between predatory sequences of *Metleucauge kompirensis* used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Hem = Hemiptera, Hym = Hymenoptera, Ple = Plecoptera, Odo = Odonata, Ort = Orthoptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded: = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

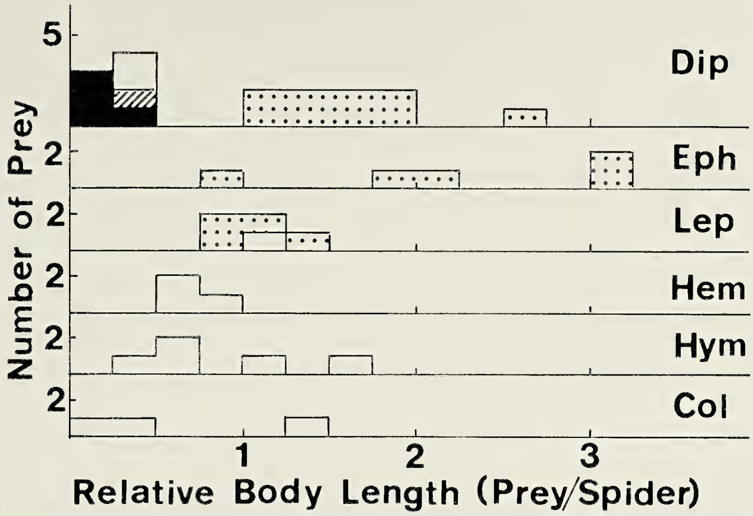

Figure 2.—The relation between predatory sequences of *Metleucauge yunohamensis* used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Hem = Hemiptera, Hym = Hymenoptera, Col = Coleoptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

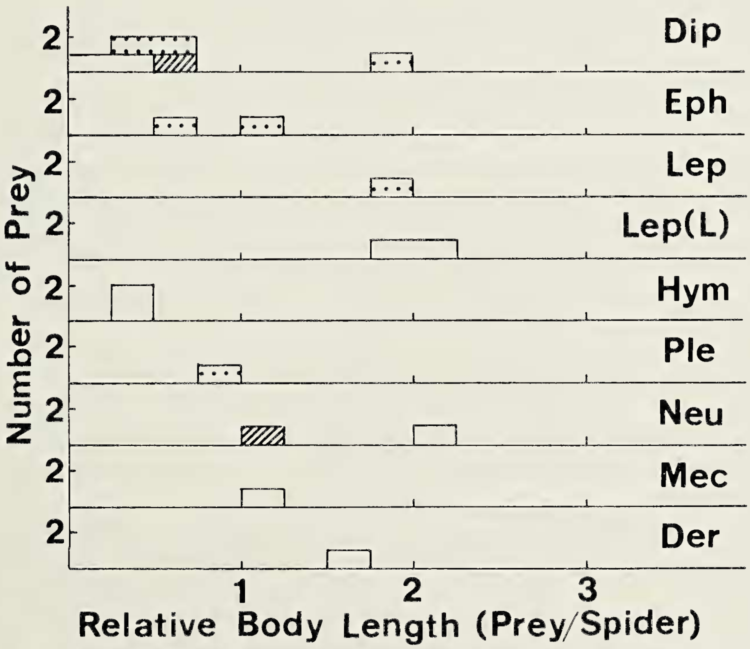

Figure 3.—The relation between predatory sequences of *Metleucauge* sp. used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Lep(L) = Lepidoptera (larva), Hym = Hymenoptera, Ple = Plecoptera, Neu = Neuroptera, Mec = Mecoptera, Der = Dermaptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

Table 3.—Prey collected in the webs of *Metleucauge kompirensis.*

Prey	Body length in mm							Total
	0–2.0	–4.0	–6.0	–8.0	–10.0	–12.0	>12.0	(%)
Diptera								
Nematocera	4023	559	24	5	0	1	0	4612(91.7)
Brachycera	7	3	1	0	0	0	0	11(0.2)
Hemiptera	85	25	0	0	0	0	0	110(2.2)
Ephemeroptera	6	103	134	22	4	2	3	274(5.4)
Plecoptera	0	3	0	3	0	0	0	6(0.1)
Hymenoptera	7	1	0	0	0	0	0	8(0.2)
Psocoptera	1	0	0	0	0	0	0	1(0.0)
Trichoptera	0	0	1	0	0	0	0	1(0.0)
Collembola	5	0	0	0	0	0	0	5(0.1)
Acarina	1	0	0	0	0	0	0	1(0.0)
Araneae	1	0	0	0	0	0	0	1(0.0)
Total	4136	694	160	30	4	3	3	5030
(%)	(82.2)	(13.8)	(3.2)	(0.5)	(0.1)	(0.1)	(0.1)	

the case of Odonata given to *M. kompirensis* and Lepidoptera to *M. yunohamensis*, there was no clear trend in relation to size. Likewise, the low capture efficiency of Hemiptera, Orthoptera, Hymenoptera, and Coleoptera, was not always dependent on prey size. For example, Hemiptera were not captured at all in spite of their small size.

The prey collected in the webs of *M. kompirensis* and *M. yunohamensis*.— Table 3 shows the prey collected from April to July in the webs of *M. kompirensis.* Of 5030 prey, dipteran insects totalled 4623 (91.9%). Almost all Diptera belonged to Nematocera. Thus, nematocerous flies are the main prey of the spider. Aside from Diptera, Ephemeroptera (mayflies) and Hemiptera (winged aphids) were relatively abundant. Other prey occurred rarely, such as Plecoptera, Hymenoptera and Collembola. These prey were generally small (96% of them were smaller than 4 mm in body length), though Ephemeroptera were relatively larger than the other prey. Potentially dangerous insects, such as wasps and pentatomids, were not collected at all, though tiny braconids were collected in small numbers.

Table 4 shows the prey collected in May in the webs of *M. yunohamensis.* Though the number of prey collected was smaller, it shows a similar trend as *M. kompirensis* (Table 1). That is, the main prey items were nematocerous flies; Ephemeroptera was the next abundant prey; the prey were generally small except for Ephemeroptera.

I could not collect the prey in the webs of *Metleucauge* sp. because the density of the webs was very low and I had not enough time to collect the prey.

DISCUSSION

Levi (1980) regarded *Meta* and the related genera as primitive in Araneidae, judging from several morphological and behavioral characters, such as eye placement, eye structure, male palpi, female genitalia and mating behavior.

This study showed that *Metleucauge* used three predatory sequences (seize-pull out, bite-pull out, and bite-wrap). Which sequence is used is generally dependent

Table 4.—Prey collected in the webs of *Metleucauge yunohamensis.*

Prey	Body Length in mm							Total
	0–2.5	–5.0	–7.5	–10.0	–12.5	–15.0	>15.0	(%)
Diptera								
Nematocera	529	28	0	0	0	1	0	558(84.7)
Brachycera	2	0	0	0	0	0	0	2(0.3)
Hemiptera	2	0	0	0	0	0	0	2(0.3)
Ephemeroptera	1	21	56	10	4	1	3	96(14.6)
Lepidoptera	1	0	0	0	0	0	0	1(0.2)
Total	535	49	56	10	4	2	3	659
(%)	(81.2)	(7.4)	(8.5)	(1.5)	(0.6)	(0.3)	(0.5)	

on prey size, that is, seize-pull out is used for small prey, on the contrary, bite-wrap for larger prey. Body weight, not body length, of the prey will have to be measured in order to acertain the accurate limits for which a different sequence is used. The spiders may decide whether the prey should be captured or not by touching it with legs I. The lack of attack wrapping is another remarkable characteristic of the predatory behavior of *Metleucauge.*

Although the predatory behavior in Metinae has not been studied in detail, Eberhard (1982) found that *Leucauge* spp. and *Chrysometa* spp. used attack (=immobilization) wrapping. *Leucauge magnifica* also often uses attack wrapping (Yoshida, unpub. data). The lack of attack wrapping of three Japanese species of *Metleucauge* therefore may suggest that Metinae represent the primitive evolutionary stages of predatory behavior (Robinson et al. 1969). This behavioral primitiveness is consistent with the primitiveness of other morphological and behavioral characters (Levi 1980). The lack of attack wrapping can be also explained in another manner, that is, the habit may have been lost secondarily (Levi 1985).

Robinson (1975) listed two merits of attack wrapping: one is the economy of the time absent from the hub, and another is the ability to attack large and/or potentially dangerous prey without the dangers involved in the intimate contact of a biting attack. Furthermore, he said that attack wrapping is never lost because its merits were too large. By which manner can the lack of attack wrapping in *Metleucauge* be explained?

The three Japanese species of *Metleucauge* usually make their webs above mountain streams, as shown earlier, and the fourth species, *M. eldorado*, also "makes an orb—between rocks near streams" (Levi 1980). Many insects (mayflies, midges, stoneflies, caddisflies, damselflies, dragonflies) fly above streams. As shown in the results, the main prey of *M. kompirensis* and *M. yunohamensis* are mayflies and midges. Eberhard (personal communication) pointed out that the prey left in the webs may not be the main prey if they are not attacked by the spiders. However, *M. kompirensis* actually feeds mainly on midges and mayflies based on my many observations. These insects are weak fliers, and can be immobilized easily by biting without danger. *Metleucauge* species seem to be accustomed to handling these insects, since the spiders ran to the prey rapidly and without hesitating when mayflies or midges were caught in their webs. Other insects flying above streams are rarely captured by the webs. For example, there are many agriid damselflies in the habitat of *M. kompirensis*, but I saw them captured only a few times during several years of investigation.

When presented with an unusual prey, not normally trapped under natural conditions (such as pentatomids or grasshoppers), the spiders approached slowly and hesitantly to the prey, often touching the prey with legs I. This suggests that *Metleucauge* species are not accustomed to such types of prey.

Another merit of attack wrapping, economy of time away from the hub, seems to be a lesser difficulty for these species. Because mayflies and midges are frequently captured, and are firmly restrained by the webs, the spiders need not handle the prey in a hurry in order to capture the next prey. Given these conditions, the ability to attack wrap may have been lost. This discussion suggests that if the ancestor of *Metleucauge* had the ability to attack wrap, and if potentially dangerous prey were included in the prey, the ability may have not been lost. In this respect, it is important to acertain whether the species of *Meta* and *Metellina* can attack wrap prey, and also, what kinds of prey they eat in nature. During 1987 I conducted a preliminary investigation of the predatory behavior of *Meta reticuloides* and found that some spiders attempted to immobilize an ant by wrapping. It appears that species related to *Metleucauge* may have the ability to attack wrap and that this may result from a difference in prey items. The predatory behavior of *Meta* and *Metellina* must be studied and be compared with that of *Metleucauge*.

If attack wrapping was fully developed (as seen, for example, in *Argiope*) in the ancestor of *Metleucauge*, this ability may not have been lost. But, if the ability was incomplete in its development, as occurs in *Leucauge magnifica* (Yoshida, unpub. data), and if incomplete ability does not have much advantage, it may have been easily lost. Other spiders such as *Mastophora* and *Dichrostichus* may also have lost attack wrapping because all the prey are non-dangerous moths and must be captured rapidly (Eberhard, pers. comm.).

I can not decide now whether the lack of attack wrapping is a primitive character or has been lost secondarily. Thorough study of the predatory behavior of genera related to *Metleucauge* (*Meta, Metellina, Chrysometa* and *Homalometa*) may solve this question.

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